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Osteology of *Squalidus multimaculatus* (Teleostei, Cyprinidae), with comments on Korean *Squalidus* zoogeography

by Kazumi Hosoya and San-Rin Jeon

Abstract. — The osteology of *Squalidus multimaculatus* is described from the neurocranium to the caudal complex. Its apomorphic features involve such characters as : the fusion between the first hypural bone and the parhypural; the lateral projection of the urohyal; the presence of a supraethmoid-frontal gap on the neurocranium; the separation of the dermal element from the basal lachrymal lamina at the anterior end of the infraorbital sensory canal. *S. multimaculatus* is the most closely related to *S. gracilis*. The zoogeography of *Squalidus* in the Korean Peninsula is also discussed.

Résumé. — L'ostéologie de *Squalidus multimaculatus* est décrite du neurocrâne au complexe caudal. Ses traits apomorphiques comprennent les caractéristiques suivantes : la fusion entre le premier hypural et la parhypural; la projection latérale de l'urohyal; la présence de la fente entre le supraethmoïde et le frontal dans le neurocrâne; la séparation de l'élément dermique de la base lacrymale laminaire à l'extrémité antérieure du canal sous-orbitaire. *S. multimaculatus* est l'espèce-sœur de *S. gracilis*, composant une unité monophylogénique. La zoogéographie de *Squalidus* dans la Péninsule de Corée est aussi discutée.

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The cyprinid genus *Squalidus* comprises six species : *S. chankaensis* Dybowski, 1872, *S. gracilis* (Temminck and Schlegel, 1846), *S. japonicus* (Sauvage, 1883), *S. iijimae* (Oshima, 1919), *S. intermedius* (Nichols, 1929) and *S. multimaculatus* Hosoya and Jeon, 1984. These species occur in rivers and lakes of the Amur Basin, Japan, the Korean Peninsula, Taiwan and North Vietnam. *Squalidus multimaculatus* was newly described from several specimens from small rivers on the eastern slope of the Taebaik Mountain Chain, Korea. Although it shows some primitive external characters (e.g., cloudy speckles on dorsum and a series of 6-12 small rounded dark spost on sides), its true systematic position is unclear, because there has been no detailed study of anatomy of this species. The purpose of this study is to describe the osteological features of *S. multimaculatus* and discuss its systematic position.

Methods and materials

Our phylogenetic analysis is based upon cladistics. The polarity is determined according to the principle of out-group comparison (Watrous and Wheeler, 1981), chiefly from the most closely related out-group of *Squalidus*, corresponding to the genus *Gobio* (Banarescu and NALBANT, 1964; HOSOYA, 1986). The rule of parsimony is adopted in order to reconstruct the most reasonable representation of the phylogeny of *Squalidus*.

Osteological and cartilaginous skeletal systems were examined in cleared and counterstained specimens prepared in a modified version of the alizarin Red S-alcian blue method of DINGERKUS and UHLER (1977) : materials were bleached by treatment with alkaline H_2O_2 before staining according to the procedure of PARK and KIM (1984) and macerated in 1-4 % KOH solution instead of trypsine. Osteological terminology follows HARRINGTON (1955).

PATTERSON (1975), HOWES (1980) and FINK and FINK (1981) were also referred to in some anatomical units (i.e., braincase and anterior vertebral region). Special attention was paid to the histological distinction of the bone, viz. dermal-, membrane- and cartilage bones according to PATTERSON (1977).

Specimens examined are deposited in the following institutions : Department of Fisheries, Faculty of Agriculture, Kyoto University, Kyoto (FAKU); Muséum national d'Histoire naturelle, Paris (MNHN); National Science Museum, Tokyo (NSMT).

MATERIAL EXAMINED

Squalidus multimaculatus : MNHN 1983-630-631, 2 specimens, 43.2-46.4 mm SL, Yongdok'oship-river, Namsam-dong, Yongdok-up, Kyongsangbuk-do, Korea; FAKU 52310, 52312, 52315, 3 specimens 27.9-49.1 mm SL, Ch'uksan-river, Togok-ri, Ch'uksan-myon, Yongdok-gun, Kyongsangbuk-do, Korea.

COMPARATIVE MATERIAL

S. gracilis gracilis : FAKU 52560-52569, 19.3-44.1 mm SL, Harai River, Iochi, Kongozaka, Meiwa-cho, Taki-gun, Mie Pref., Japan; FAKU 52106, 1 specimen, 66.1 mm SL, Taki River, Hayashino, Mimasaka-cho, Aida-gun, Okayama Pref., Japan; FAKU 51218, 1 specimen, 52.9 mm SL, Yoshii River, Kagamino-cho, Tomada-gun, Okayama Pref., Japan; FAKU 52576-52596, 21 specimens, 45.1-65.9 mm SL, Midori River, Nishihara-mura, Kikuchi-gun, Kumamoto Pref., Japan.

S. gracilis majimae : FAKU 52319, 52332, 52334, 52339, 52345, 5 specimens, 49.1-67.9 mm SL, Somjin-river system Maryong-river, Kyeso-ri, Maryong-myon, Chin'an-gun, Chollabuk-do, Korea.

S. japonicus japonicus : FAKU 52307-52309, 3 specimens, 46.1-62.1 mm SL, Lake Biwa, Shina, Kusatsu, Shiga Pref., Japan.

S. japonicus coreanus : FAKU 54814, 1 specimen, 55.2 mm SL, Han river, Ich'on-dong, Yongsan-gu, Seoul, Korea.

S. chankaensis chankaensis : FAKU 50440-50442, 3 specimens, 60.0-70.6 mm SL, Wudairen-chi, Heirong-chiang, China.

S. chankaensis biwae : FAKU 52190-52284, 95 specimens, 40.2-94.7 mm SL, Lake Biwa, Hamabun, Imazu-cho, Shiga Pref., Japan.

S. chankaensis argentatus : MNHN 34-57, 59, 1 specimen, 60.4 mm SL, Chekiang, China.

S. chankaensis wolterstorfii : FAKU 50462, 1 specimen, 75.9 mm SL, Cho-gan, Fukien, China.

S. chankaensis tsuchigae : FAKU 54815, 1 specimen, 65.4 mm SL, Miryang-river, Miryang-gun, Kyongsangnam-do, Korea.

S. iijimae : FAKU 52556, 1 specimen, 63.2 mm SL, Shin-den Shih, Taipei, Taiwan.

S. intermedius : FAKU 50445, 1 specimen, 52.4 mm SL, Lower Hwang-ho, Tsinan, Shagtung, China.

Gobio gobio gobio : NSMT-P 27648, 1 specimen, 72.0 mm SL, River Don, Voronezh, Rossiskauya, SFSR, USSR.

G. gobio soldatovi : NSMT-P 16224, 1 specimen, 90.4 mm SL, River Amur, Takhta, Rossiskaya, SFSR, USSR.

G. kessleri banaticus : NSMT-P 13771, 13772, 2 specimens, 55.7-60.1 mm SL, River Timis, Albina, Timosoara Bant, Rumania.

OSTEOLOGICAL DESCRIPTION

Neurocranium

Neurocranium similar to that of *Gobio gobio* (Vandewalle, 1974, 1975), with the subtriangular dorsal outline and dorsal deep insertion of the supraoccipital into the posterior parietal joint (fig. 1). Ethmoid cartilage (ec) well developed, anteriorly, covering irregular hemispherical preethmoid. Supraethmoid (SE) wide, with a medial depression on its dorsal surface. Anterior border of supraethmoid slightly notched, the posterior border sutured with frontals (F) only at the corners to form the unossified supraethmoid-frontal gap (sfg). This gap still visible even in adults. The lateral concavities of both frontal deep, the minimum width of the interorbital region reduced to approximately half of the widest part of the frontals. Mesethmoid (ME) underlying supraethmoid; its sloped concavity continued to supraethmoid notch; posterior border of mesethmoid wall deeply notched to form anterior part of heart-shaped foramen. Each lateral ethmoid (LE) anteriorly cartilaginous, forming posterior part of the foramen; ventrally, posterior margin of lateral ethmoid with a pair of small cartilaginous facets for articulation with suspensorium. Vomer (VO) moderately short, and overlain anteriorly by ethmoid, and posteriorly by parasphenoid. Orbitosphenoids (OS) deep, and ventromedially joined to each other to form an interorbital septum. Pterosphenoid (PTS) not in contact with parasphenoid. Parasphenoid (PS) with posterolateral ascending wings; dorsal edges of the wings sutured posteriorly with prootics. Enlarged carotid foramen situated along the suture. Optic foramen surrounded by orbitosphenoid base in its anteriormost portion. Prootic (PRO) large with its anterior margin concave laterally, forming lateral commisure (lc); lateral jugular bridge (terminology, see Howes, 1980) absent on the bone; dorsally, prootic bordered by sphenotic (SP). Sphenotic lateral projections short. Hyomandibular fossa surrounded anteriorly by sphenotic, and posteriorly by pterotic (P). Posterolateral tip of each pterotic spinous; its inner concavity carrying a small ossification, the intercalar (IC); pterotic spine well separated from exoccipital margin. Subtemporal fossae deep, and bounded by prootic, pterotic and exoccipital (EXO) and connected directly to posttemporal through a narrow slit. Epiotic (EP) lateral face roofing posttemporal fossa. Nasal (N) tubular in shape; four sensory pores opening in it, including both ends; anterolaterally, the bone well separated from supraethmoid. Supraorbital (SOR) oval in dorsal profile. No fontanelle on skull roof of adults, though present between parietals (PAR) in younger fish (FAKU 52315, 27.9 mm SL). Anterior portion of supraoccipital (SO) on a raised platform, and its sides contributed by parietals; supraoccipital crest moderately high. Lateral occipital fenestra present in exoccipital (EXO). Masticatory plate of basioccipital (BO) rather underdeveloped.

Jaws

Upper jaw highly protrusible. Ascending process of premaxillary (fig. 2 A, PMX) long; no special articulation present along medial attachment. Lower margin of maxilla (MAX) slightly sloping. Dorsal curvature of kinethmoid (KE) expanded into two heads. Dentary (D) and anguloarticular (AA) forming deeply interlocking joint. Dentary coronoid process

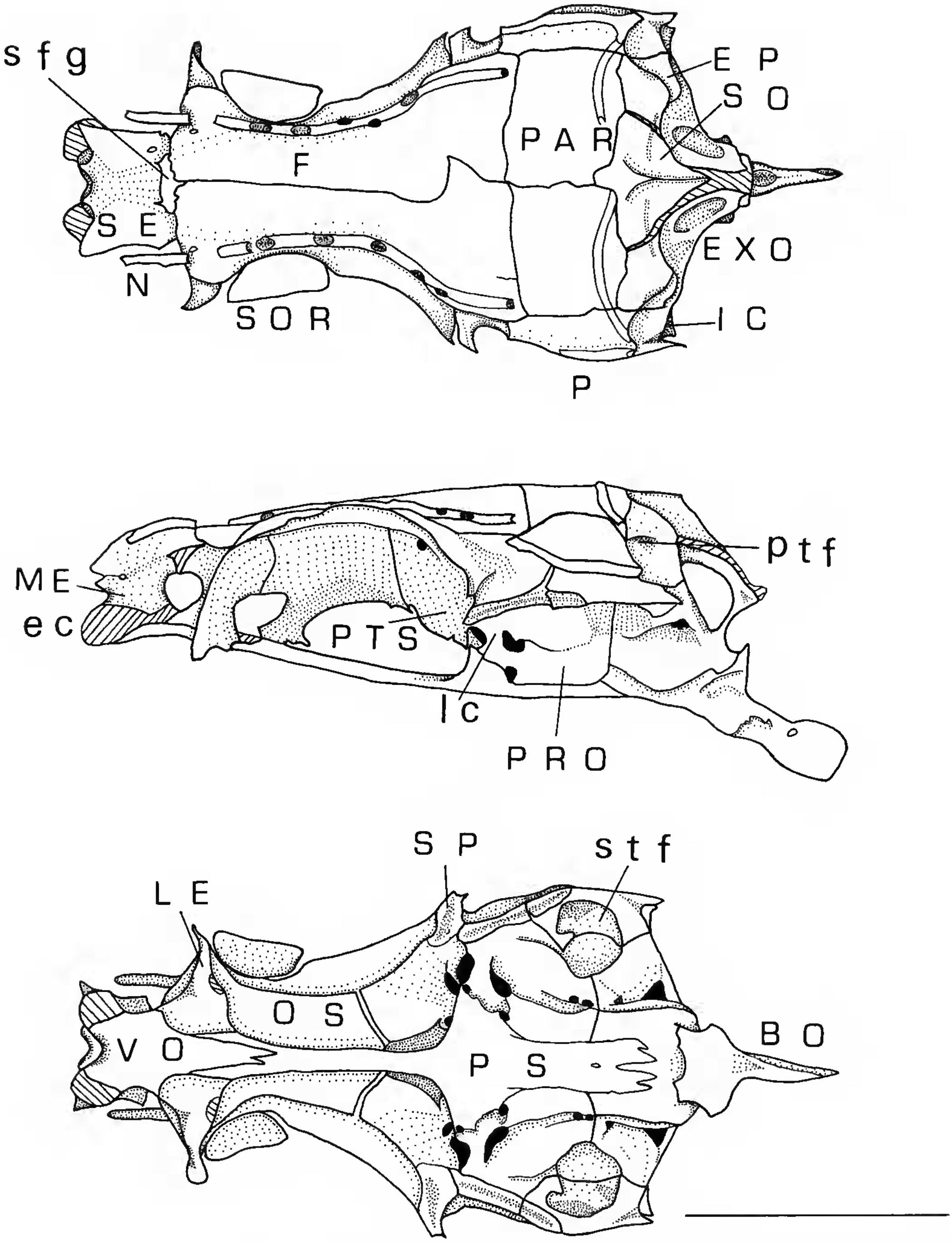

Fig. 1. — Neurocranium of *Squalidus multimaculatus*. Dorsal, lateral and ventral views from top to bottom. Cartilage is cross-hatched. Scale indicates 3 mm. BO, basioccipital; ec, ethmoid cartilage; EP, epiotic; EXO, exoccipital; F, frontal; IC, intercalar; lc, lateral commisure; LE, lateral ethmoid; ME, mesethmoid; N, nasal; OS, orbitosphenoid; PAR, parietal; P, pterotic; PRO, prootic; PS, parasphenoid; ptf, posttemporal fossa; PTS, pterosphenoid; SE, supraethmoid; sfg, supraethmoid-frontal gap; SOC, supraoccipital; SOR, supraorbital; SP, sphenotic; stf, subtemporal fossa; VO, vomer.

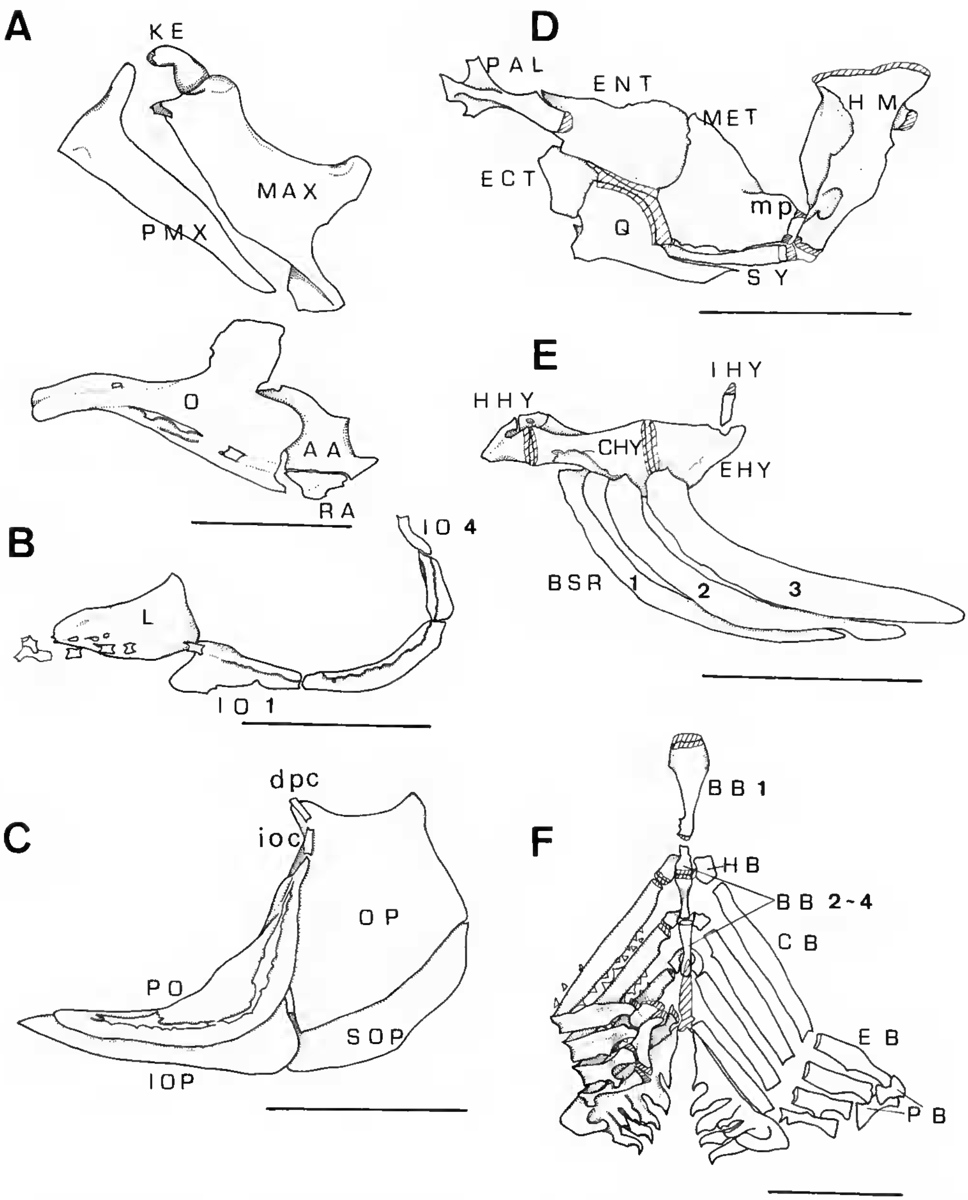

FIG. 2. — Skeletal systems of the head region of *Squalidus multimaculatus*. A, jaws; B, infraorbital series; C, opercles; D, suspensorium; E, hyoid arch; F, branchial arch. A-E, lateral view; F, dorsal view. Cartilage is cross-hatched. Scales indicate 3 mm. AA, anguloarticular; BB, basibranchial; BSR, branchiostegal ray; CB, ceratobranchial; CHY, ceratohyal; D, dentary; dpc, dermopterotic canal; EB, epibranchial; ECT, ectopterygoid; EHY, epihyal; ENT, entopterygoid; HB, hypobranchial; HHY, hypohyal; HM, hyomandibular; IHY, interhyal; IO, infraorbital; ioc, intramural opercular canal; IOP, interopercle; KE, kinethmoid; L, lachrymal; MAX, maxillary; MET, mepapterygoid; mp, metapterygoid process; OP, opercle; PAL, palatine; PB, pharyngobranchial; PMX, premaxillary; PO, preopercle; Q, quadrate; RA, retroarticular; SOP, subopercle; SY, symplectic.

moderately high. Anguloarticular with Meckelian cartilage anteriormost, coronomeckelian on its inner side, and retroarticular (RA) on its lower margin.

Infraorbital and opercular series

Lachrymal (L), subtriangular, and the largest bone in the infraorbital series (fig. 2 B). Anterior end of infraorbital canal situated on an unossified lamina. Fourth infraorbital (IO 4) represented by a membranous canal only.

Preopercle (PO) broadly crescentic bearing the preopercular canal (fig. 2 C). Interopercle (IOP) longer with a ventral ramus extending more anteriorly than preopercle. Opercle (OP) large bearing two ossified canals aligned in a vertical line : upper, dermopterotic canal (dpc); lower, intramural opercular canal (ioc) (see HOWES, 1981). Subopercle (SOP) narrow, forming ventral gill cover together with branchiostegal rays.

Suspensorium

Suspensorium (fig. 2 D) elongate, articulating with neurocranium through palatine and hyomandibular. Posterior edge of palatine (PAL) cartilaginous, articulating with the entopterygoid (ENP). Ectopterygoid (ECT) irregularly squarish in shape. Anterior margin of metapterygoid (MET) extending dorsad, to cover whole posterior margin of entopterygoid; posteriorly, metapterygoid having two small cartilaginous projections at upper and lower tips. Metapterygoid process (mp, see HOWES, 1978) poorly developed. A narrow horizontal gap present between metapterygoid and sympletic (SY). Quadrate (Q) internally, inserted by symplectic. Hyomandibular (HM) articulating with a fossa on neurocranium by its double head.

Hyoid and branchial arches

Ceratohyal (CHY) connected by cartilage, anteriorly with upper and lower hypohyal (HHY), and posteriorly with triangular epihyal (EHY) (fig. 2 E). Posterodorsal margin of epihyal concave, for interhyal (IHY) articulation. First branchiostegal (BSR 1) attached to inside of ceratohyal; second (BSR 2) to outside of the bone; third (BSR 3) to outside of ceratohyal-epihyal suture. Urohyal (fig. 3) irregular and rhomboid in shape, bifurcated anteriorly, and having a pair of anterolateral wings, each with a lateral projection (ulp) to accommodate sternohyoides; urohyalar dorsal edge notched to half way.

Anterior portion of first basibranchial (BB 1) expanded laterally (fig. 2 F). Posteromedially, three rod-like basibranchials (BB 2-4) and one posterior cartilaginous copula aligned. Each articulation surrounded by a pair of hypobranchials (HB); ventrally, first pair separated from each other, while second and third pairs fused their partners respectively. Four pairs of ceratobranchials (CB) elongate. Four pairs of epibranchials (EB); third epibranchial expanded into double head. First pharyngobranchial (PB) absent, second and third present. Two rows of pharyngeal teeth, with a dental formula 3.5-5.3; first tooth of main row long, pointed, and moderately compressed with oblique grinding surface.

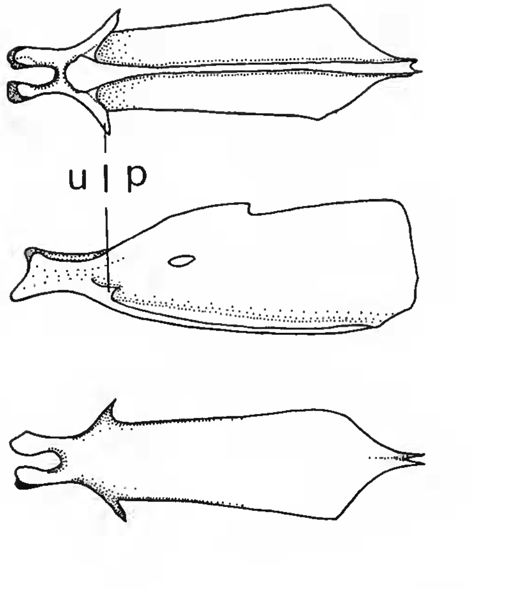

FIG. 3. — Urohyal of *Squalidus multimaculatus*. Dorsal, lateral and ventral views from top to bottom. Scale indicates 3 mm. ulp, urohyalar lateral projection.

Appendicular skeleton

In anterior vertebrate, Weberian apparatus (fig. 4 A) composed of claustrum (CLA), scaphium (SCA), intercalarium (INC), and tripus (TR); each element connected by a ligament. Second centrum not fused to third. Synchondral joint (scj, see FINK and FINK, 1981) intercalating supraneurals (SN), third neural arch (NA) and fourth. Os suspensorium (os) long and ventrally tapered to meet its fellow.

In pectoral girdle, supratemporal tubular, with three pores interceding infraorbital canal and supratemporal canal for lateral-line. Posttemporal triangular, with a poorly ossified canal bone (lateral extrascapular of LEKANDER, 1949; RAMASWAMI, 1952*a*, *b*, 1953) attaching to epioccipital and pterotic anteriorly. Supracleithrum, blade-like, with a canal bone as well. Cleithrum (CL) the largest in the girdle; its medial ridge sloped to mesocoracoid arch (fig. 4 B). Mesocoracoid (MC) base supported by both coracoid (CR) and scapula (SCP). Postcleithrum long. Four radials (R); six accessory cartilages between radials and pectoral fin rays.

In pelvic girdle, no opening on flat dorsal plane of pelvic bone (fig. 4 C); outer process of pelvic bone longer than medial process; its anterior tip truncated and cartilaginous. A splint bone present in lateral side of the girdle.

In dorsal fin support (fig. 4 D), nine proximal pterygiophores (PP), including a terminal stay (STY); five medials (MP); eight distals (DP). These pterygiophores arranged in a serial articulation; anterior most three series lacking medial.

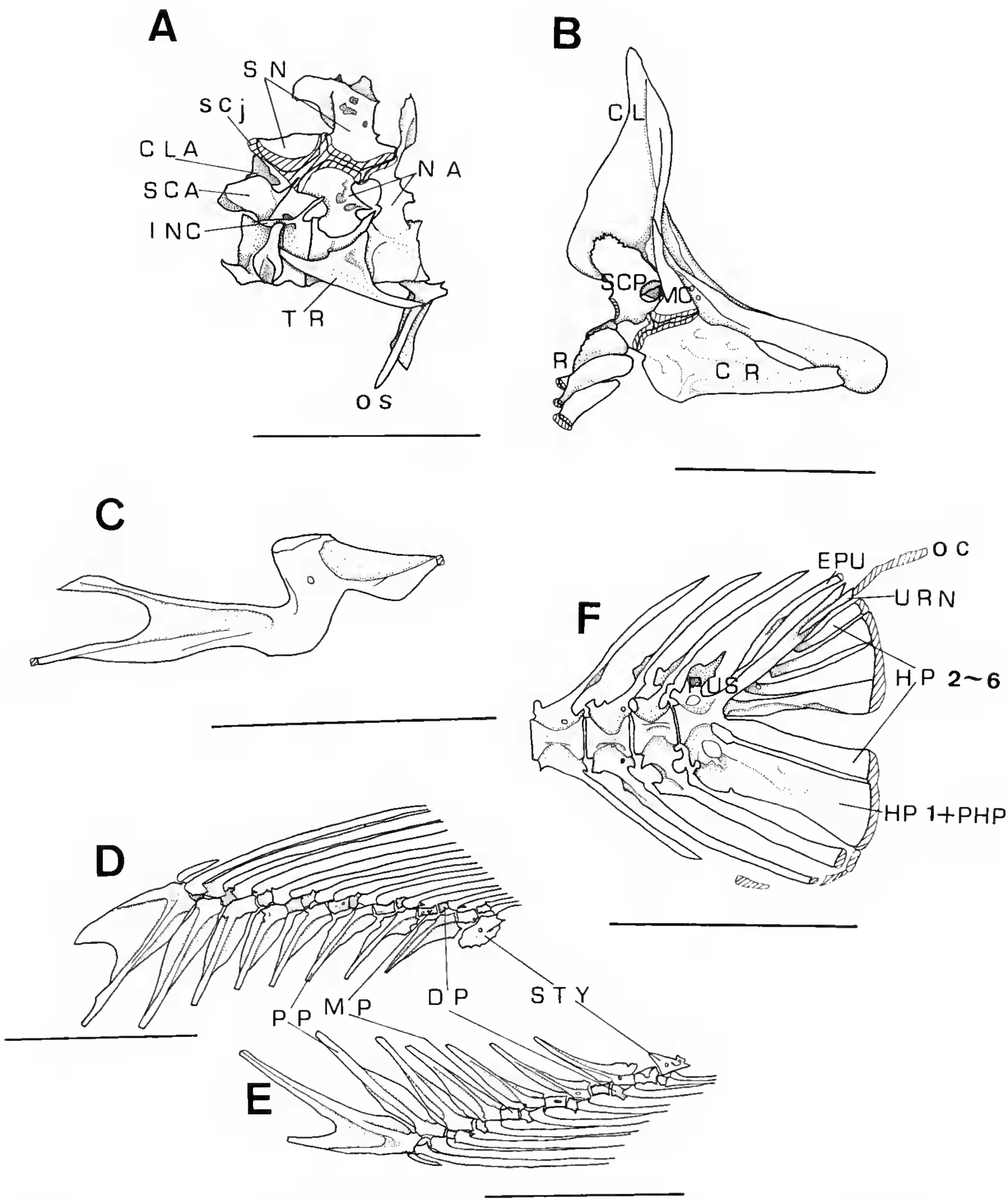

FIG. 4. — Axial and appendicular skeleton of *Squalidus multimaculatus*. A, anterior vertebrae; B, left pectoral girdle; C, left pelvic girdle; D, dorsal fin support; E, anal fin support; F, caudal complex. A, B and D to F, lateral view; C, dorsal view. Cartilage is cross-hatched. Scales indicate 3 mm. In B postcleithrum is removed. CL, cleithrum; CLA, claustrum; CR, coracoid; DP, distal pterygiophore; EPU, epural; HP, hypural; INC, intercalarium; MC, mesocoracoid; MP, median pterygiophore; NA, neural arch; oc, opisthural cartilage; os, os suspensorium; PHP, parhypural; PP, proximal pterygiophore; PUS, pleurostyle; R, radial, SCA, scaphium; scj, synchondral joint; SCP, scaphium; SN, supraneural; STY, stay; TR, tripus; URN, uroneural.

In anal fin support (fig. 4 E), eight proximal pterygiophores; four medials; seven distals. Articulatory pattern of each pterygiophore same as dorsal fin support.

In caudal complex, posterior margin covered with cartilaginous membrane (fig. 4 F). Epural (EPU) long. Pleurostyle (PUS, terminology, see Dunn, 1983) elongated, with a pair of uroneurals (URN) on its distal side; the bone posteriorly displaced by opisthural cartilage (oc). Four hypurals (HP) in upper half plate, two in lower. First hypural firmly fused parhypural (PHP).

DISCUSSION

Character state of *S. multimaculatus*

The skeletal system of *S. multimaculatus* accord well with the basic gobionine features (sensu Hosoya, 1986) characterized by several synapomorphies : the supraoccipital bone wedges the posterior margin of the parietals on the dorsal plane of the neurocranium; the lateral concavities of the frontals are deep so that the minimum interorbital width of the frontals is reduced to approximately half of the widest part of the frontals.

Also, *S. multimaculatus* displays some derived features. One of them are common to other *Squalidus* members, and the generic outgroup *Gobio* : (1) Two rows of pharyngeal teeth.

(2) Fusion between the first hypural and the parhypural can be observed in all the *Squalidus* species examined here. This is a remarkable generic autapomorphy to distinguish *Squalidus* as a monophyletic group, not only from other gobionine genera, but also *Gnathopogon* which is often regarded as congeneric as *Squalidus* (Okada, 1960; Lo *et al.*, 1977).

(3) Lateral projection of the urohyal and (4) supraethmoid-frontal gap on the neurocranium, both are strong synapomorphies linking *S. multimaculatus* to *S. gracilis*. Additionally, (5) the separation of the infraorbital canal from the supraorbital canal corroborates the close phyletic relationship of both species (Hosoya and Jeon, 1984).

As for the specific autapomorphy, it is quite unique that (6) the anterior tip of the dermal canal (sensu Patterson, 1977) of infraorbital sensory system completely separated from the basal lachrymal lamina. We do not know such a condition in any other ostariophysan groups.

Compared with other *Squalidus* species, the skeletal system of *S. multimaculatus* is rather primitive as observable in the out-group in the following characters. The anterior margin of the urohyal of *S. multimaculatus* is deeply concave while (7) that of *S. chankaensis, S. japonicus, S. intermedius* and *S. iijimae* is sharply forked with two long processes which include basibranchial and hypohyal attachments respectively. First basibranchial of *S. multimaculatus* has no specialization in the way of attachment of the first basibranchial-hypohyal ligament. On the other hand, (8) the bone of *S. gracilis* has laterally the bony wing to support the ligament (fig. 5). It is comparable with the specializations in external features : (9) the enlargement of lateral-line scales, and (10) the disappearance of lateral spots on both sides. Every character state of *S. multimaculatus* above mentioned, seems to be in the plesiomorphic condition.

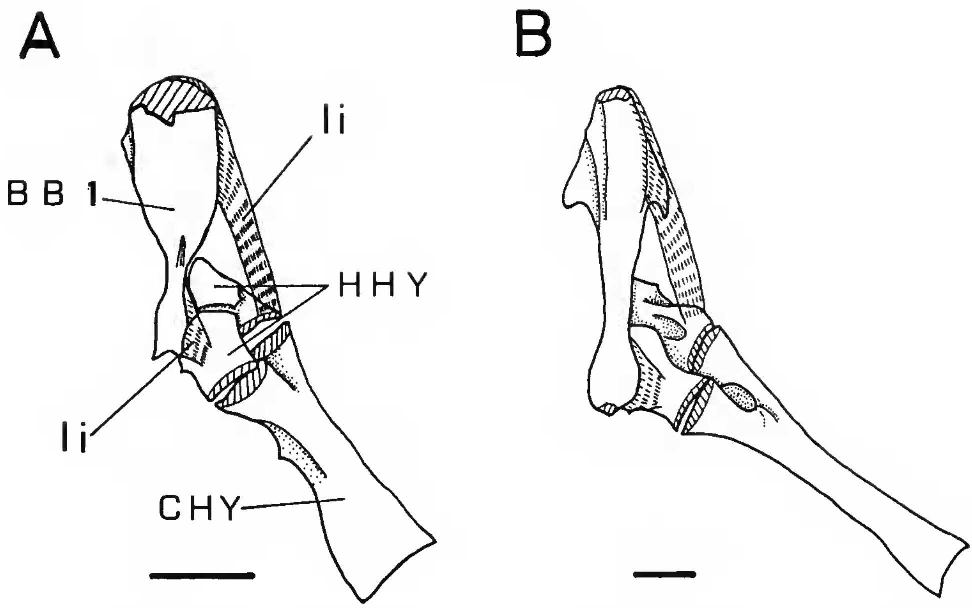

FIG. 5. — Connection between first basibranchial and hypohyal in *Squalidus*, dorsal view. A, *S. multimaculatus*; B, *S. gracilis majimae*. Cartilage is cross-hatched. Scales indicate 0.5 mm. BB 1, first basibranchial; CHY, ceratohyal; HHY, hypohyal; li, ligament.

On the basis of the character analysis, we present here the most parsimonious hypothesis of the intrageneric relationships of *Squalidus* in figure 6.

Phyletic relationships to other taxa

The genus *Squalidus* is divided into two phyletic groups, viz. the *S. gracilis* lineage and the *S. chankaensis* lineage. The former is composed of *S. multimaculatus* and its sister species *S. gracilis*, whereas the latter includes all other remaining species (*S. chankaensis, S. japonicus, S. iijimae*, and *S. intermedius*). This phyletic differentiation is accompanied with the habitat segregation. The *S. gracilis* lineage prefers to more rapid water than the *S. chankaensis* lineage. When both are sympatrically distributed, the *S. gracilis* lineage always occurs in upper reaches while the *S. chankaensis* lineage in lower reaches (HOSOYA, 1982).

Squalidus zoogeography in the Korean Peninsula

There are four living forms of *Squalidus* in the Korean Peninsula : *S. multimaculatus, S. gracilis majimae, S. chankaensis tsuchigae* and *S. japonicus coreanus* (UCHIDA, 1939; BANARESCU and NALBANT, 1973; CHOI *et al.*, 1983; HOSOYA and JEON, 1984). The distribution of *S. gracilis majimae* continues that of *S. gracilis gracilis* in the western part of Japan. *S. chankaensis tsuchigae* is the Korean representative of *S. chankaensis* which is divided into 12 subspecies, including the Chinese *S. chankaensis chankaensis* and the Japanese *S. chankaensis*

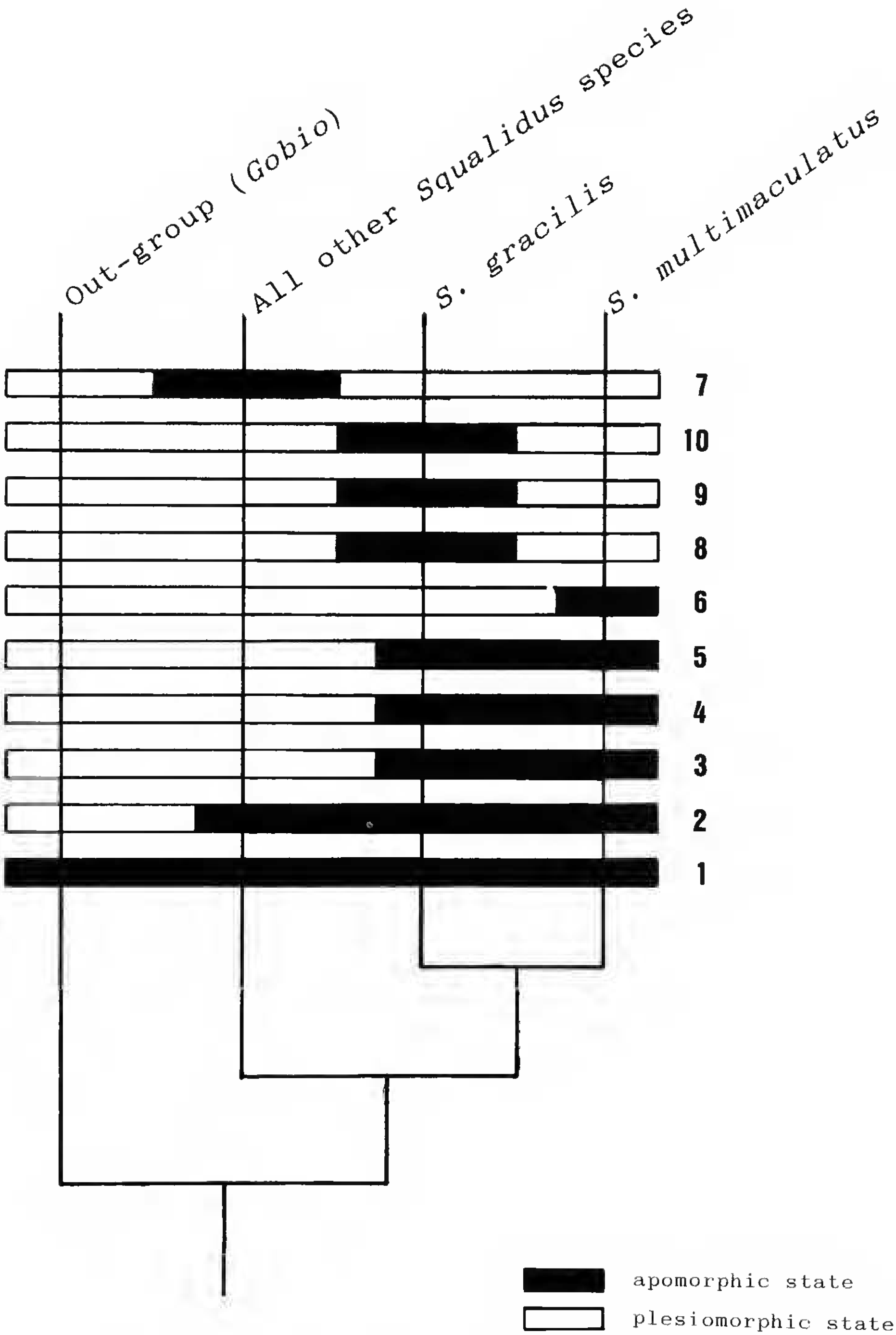

FIG. 6. — Cladogram of the most parsimonious of relationships in hte genus *Squalidus* with the character distribution. The synapomorphies of the numbered characters are (1) two rows of pharyngeal teeth, (2) the fusion between the first hypural and the parhypural, (3) the lateral projection of the urohyal, (4) the supraethmoid-frontal gap on the neurocranium, (5) the separation of the infraorbital canal from the supraorbital canal, (6) the separation of the anterior tip of the dermal sensory canal from the basal lachrymal lamina, (7) the long anterior processes of the urohyal, (8) the lateral bony wing of the first basibranchial, (9) the enlargement of lateral-line scales, (10) the disappearance of the lateral spots on sides.

biwae (BANARESCU, 1969; BANARESCU and NALBANT, 1964, 1973). *S. japonicus coreanus* is a single subspecies for *S. japonicus japonicus* isolated in Lake Biwa and the Nobi Plain.

In the Korean Peninsula, only *S. multimaculatus* inhabits the eastern slope of the Taebaik Mountain Chain, from Hoeya-river (35°20-22′N) to Somch'okoship-river (37°25-27′N) (fig. 7). Contrarily, *S. gracilis majimae* is distributed together with *S. chankaensis tsuchigae* and *S. japonicus coreanus* on the west side of the Chain. This distributional differentiation, bordered by the Chain, corresponds to CHOI's (1973) zoogeographic divisions. The east side is defined as the "East Korean Subdistrict" which is characterized by the Amur or Manchurian elements such primary freshwater fishes as *Phoxinus phoxinus, P. lagowskii, Noemacheilus toni*, and *Lefua costata* (CHOI, 1973; CHOI *et al.*, 1983; JEON, 1982). On the other hand, the west side is defined as "West-South Korean Subdistrict" which abounds in Chinese elements. There has been no evidence to show the sister-group relationship on every zoogeographic element between East Korean Subdistrict and West-South Korean Subdistrict. Information about the *Squalidus* distribution in the Amur drainage or Manchuria, is quite limited, however, the specimen from Jehol identified as *Gnathopogon wolterstorfii* by MORI (1934), seems to be actually a *S. multimaculatus*, having a set of diagnostic characters : a long head and a series of large lateral spots on both sides. These observations lead us to consider the dispersal from Manchuria to the east side of the Korean Peninsula as a main factor for the distributional distinction in *Squalidus*.

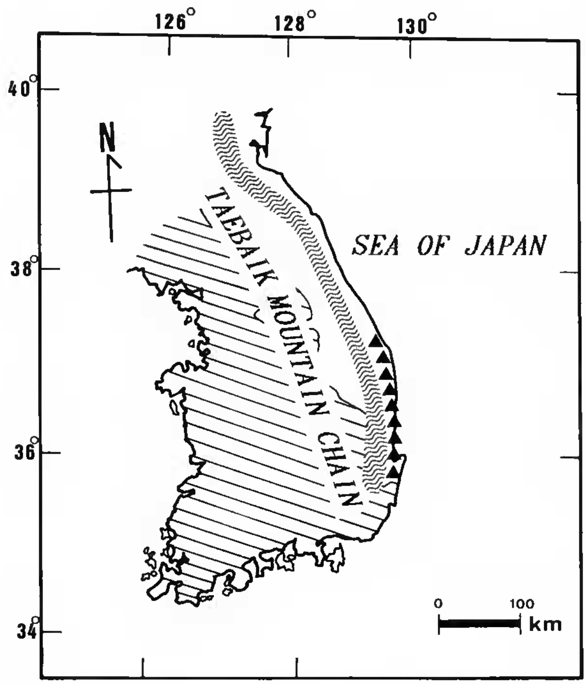

FIG. 7. — Geographic distribution of Korean *Squalidus*. Modified from HOSOYA and JEON (1984). ▲, *S. multimaculatus*; dashed area, *S. gracilis majimae, S. chankaensis tsuchigae* and *S. japonicus coreanus*.

Absence of the *S. chankaensis* lineage on the east is ecologically due to the shortage of the lower reaches of the rivers, which empty into the Sea of Japan by the length within 50 km at the steep angle. They completely lack the stagnant waters or pools with muddy bottom which is necessary to occur for the *S. chankaensis* lineage. Contrarily, sympatric distribution of *S. gracilis* with other *Squalidus* members on the west, can be explained by the large carrying capacity of the rivers represented by Han-river, Kum-river and Naktong-river.

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